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A new European species of *Mesocrina* (Hymenoptera, Braconidae, Alysiinae, Alysiini) with notes on the biology and systematics of the genus

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Abstract

Mesocrina chandleri Godfray & van Achterberg, **sp. nov.**, is described in the small Holarctic genus *Mesocrina* Foerster, 1863, the second European species. The holotype was collected in England and further specimens are recorded from Finland, France and the Netherlands. A key is provided to the Palaearctic *Mesocrina* species. DNA sequence from the CO1 barcode locus was obtained and the new species is 10% divergent from *M. indagatrix* (the other European species) and 5% divergent from an undetermined North American species. We provide evidence that *Mesocrina* spp. parasitise cyclorrhaphan Diptera in fungi (and that previous host records from phytophagous insects are incorrect) and that the taxon is not part of the *Dapsilarthra* genus-group as often previously assumed.

Keywords

DNA barcode, Europe, hosts, *Mesocrina chandleri*, Palaearctic key

Introduction

The genus *Mesocrina* Foerster, 1863 was erected for *M. indagatrix* Foerster, 1863, which for a long time was the sole member of the genus as understood today. In the last quarter of the 20th century four further species were described from the Eastern Palaearctic and India (van Achterberg 1983; Belokobylskij 1998) and two from

North America (Wharton 1980). Females of the genus are distinctive as they have a laterally compressed metasoma with dorsal carina on the third and distal tergites, but both sexes can be identified to genus relatively easily in standard keys to the Alysiini (Fischer 1971; Tobias 1986; Wharton 1997; Belokobylskij and Tobias 1998; Zhu et al. 2017).

Mesocrina indagatrix, hitherto the only species known from Europe (Königsmann 1959; van Achterberg 1983, 2014), is a widespread but uncommon species with relatively few specimens in major collections. An examination of the four *Mesocrina* in the collection of the National Museum of Scotland found that in addition to three *M. indagatrix*, there is a single female specimen that differs from *M. indagatrix* in several aspects, notably it is larger in size and has a longer ovipositor. DNA sequence from the CO1 barcode locus was obtained from both *M. indagatrix* and the aberrant specimen and were clearly distinct (10% divergence). The BOLD database contained a specimen from Finland with identical sequence to the new taxon which was borrowed and found to be a male. Four further specimens were then discovered in recent collections from the Netherlands and France. The wasps differ from the species known from the East Palaearctic and North America and here are described as belonging to a new species.

Methods

Details of the holotype and five paratypes are given below in the type designation. The holotype is deposited in the National Museum of Scotland, Edinburgh, the male paratype in the Zoological Collections of the Finnish Museum of Natural History, University of Helsinki, Finland, and the remaining paratypes in the entomological collection of the Naturalis Biodiversity Center, Leiden.

The specimen of *Mesocrina indagatrix* from which DNA sequence was obtained has the data: ♀, Savernake Forest, Wiltshire, England, United Kingdom (51.402N, 1.694E; UK Grid Reference SU214671); Malaise trap, 22 August – 25 September 1991; (collector not recorded); (Sample ID: NR1040; BOLD process ID: BRAAL476-19).

Photographs were taken through a Leica M125C microscope with focus stacking using the Leica Application Suite X (LAS X) image analysis software with final processing in Photoshop. Ratio measurements were also made using the LAS X system. Morphology terminology follows Wharton et al. (1997).

CO1 sequencing was carried out by the Biodiversity Institute of Ontario at the University of Guelph with initial Sanger sequencing supplemented in the case of the *M. indagatrix* specimen by "next generation" short read sequencing (Prosser et al. 2016). Our sequence data are publicly available at http://v4.boldsystems.org/ which also provides full details of primers. Sequence analysis was carried out on the BOLD platform and using the programme MEGA11 (Molecular Evolutionary Genetics Analysis version 11, Tamura et al. (2021)).

Systematics

***Mesocrina chandleri* Godfray & van Achterberg, sp. nov.**
https://zoobank.org/F38D6FA7-860D-4378-9150-23D8E1CF53C3
Figs 1, 2

Type material. ***Holotype***, ♀, south side of Haugh Wood, Herefordshire, England, **United Kingdom** (52.021°N, 2.600°W; UK Grid Reference SO589360); 10 October 1998; swept, P.J. Chandler; National Museum of Scotland (Sample ID: NR980; BOLD process ID: BRAAL477-19).

Paratype, ♂, near Nurmijärvi, Uusimaa, **Finland** (60.523°N, 24.842°E; Finnish Grid Reference 6711:381); 8 September 1994; Malaise Trap, M. Koponen; Finnish Museum of Natural History (MZH) (Sample ID, MZH_GQ.22; BOLD process ID: LEFIJ28469-22).

Paratype, ♀, Lac de Remoray, Doubs, **France** (46.785°N, 6.254°E; French [Lambert 93] Grid reference 948242, 6634560); 27 October 2021; Malaise Trap, H. Gens, (RMNH'23") Naturalis Biodiversity Center.

Paratypes 2 ♀, Veluvia-Hamelakkers, Wageningen, Gelderland, **The Netherlands** (51.969°N, 5.681°E); 25–29th October 2022; caught at a skylight, D. Belgers, RMNH'23"; Naturalis Biodiversity Center.

Paratype, ♀, Wassenaar, Zuid-Holland, **The Netherlands** (52.142°N, 4.379°E; Dutch [RDS] Grid reference 86.60, 462.12); 20 October 2023; on underside of *Armillaria mellea* (honey fungus), P.H. Hoekstra, RMNH'23"; Naturalis Biodiversity Center.

Name. The new species is named for Peter J. Chandler, the eminent Diptera entomologist who collected the first specimen in 1998.

Description of female holotype. ***Holotype***, ♀, length of body 3.8 mm, of fore wing 4.7 mm (Fig. 1).

Head. Antenna with 36 segments, 1.1 times length of fore wing and 1.5 times body, densely clothed with anteriorly directed setae projecting at an angle of 30°; length of third segment 0.7 times fourth segment, lengths of third, fourth and penultimate segments 3.9, 2.7 and 2.4 times their widths, respectively; maxillary and labial palps with 6 and 4 segments, respectively; length of maxillary palp ~ 2.6 times height of eye; OOL 2.3 times greater than POL, POL 1.4 times posterior ocellus diameter; in dorsal view head 2.0 times wider than maximum length, margin of temples posterior to eye slightly convex; vertex shiny with scattered anteriorly-directed setae especially near occiput and margin of eye, a weak furrow runs from between posterior ocelli to occiput; frons largely smooth and glabrous with small areas of rugosity and a small number of setae; dorsal length of eyes 0.6 times maximum length of head, glabrous; face 1.8 times wider than high medially, 0.6 times as wide as head, largely smooth with some slight rugosity medially, with moderately dense setae apart from a narrow medial glabrous band, the setae dorsally directed except at sides where they point laterally and latero-ventrally; clypeus glabrous with sparse punctures, ventral margin very slightly convex, epistomal suture distinct; malar space 0.15 times basal width of mandible; mandibles

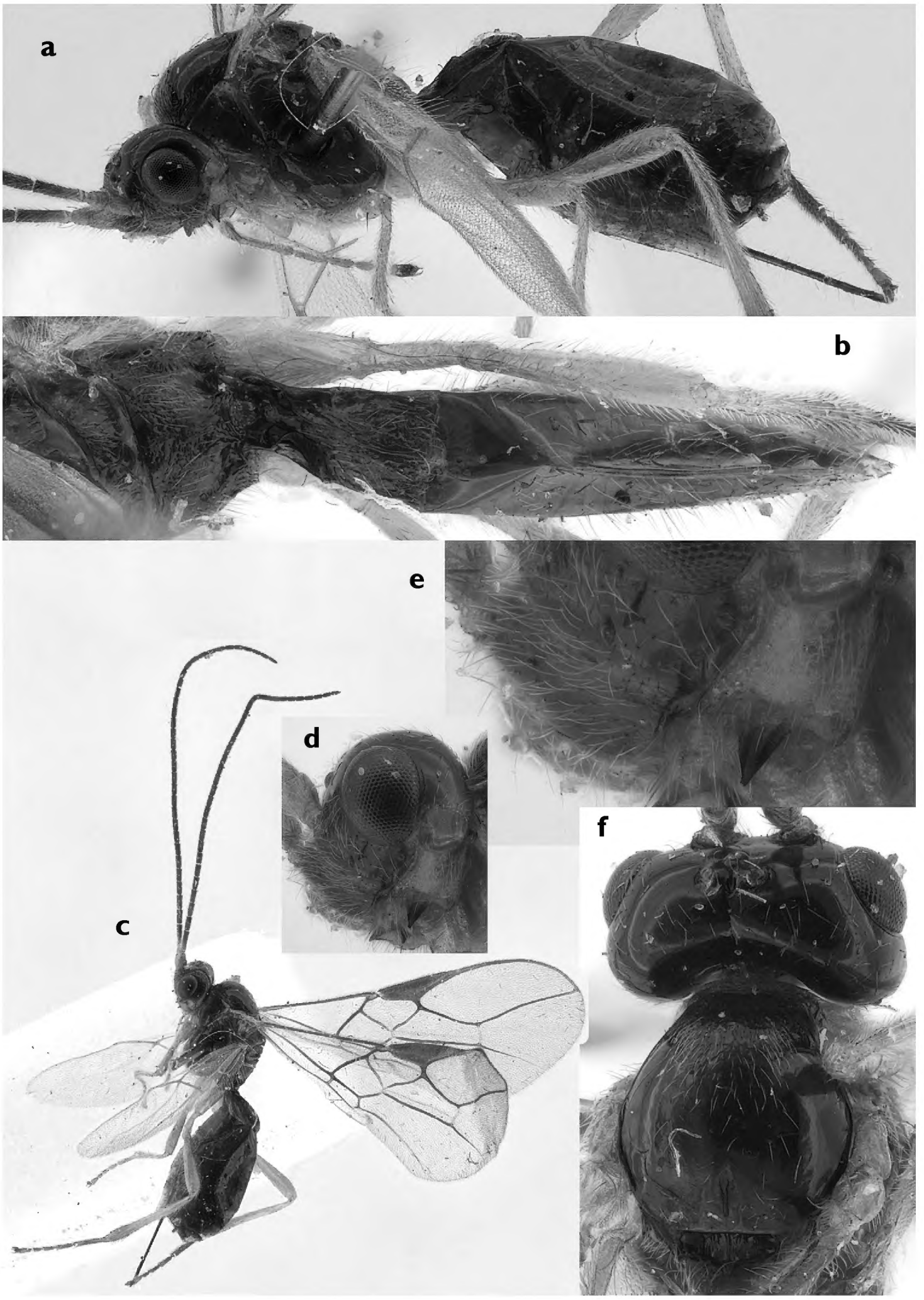

Figure 1. Montage of photographs of the female holotype (Sample ID NR890) of *M. chandleri* **a** lateral view **b** dorsal metasoma **c** whole insect **d** lateroventral head **e** face and mandible **f** dorsal head and mesosoma. The length of the body (excluding antennae and ovipositor) is 3.8 mm.

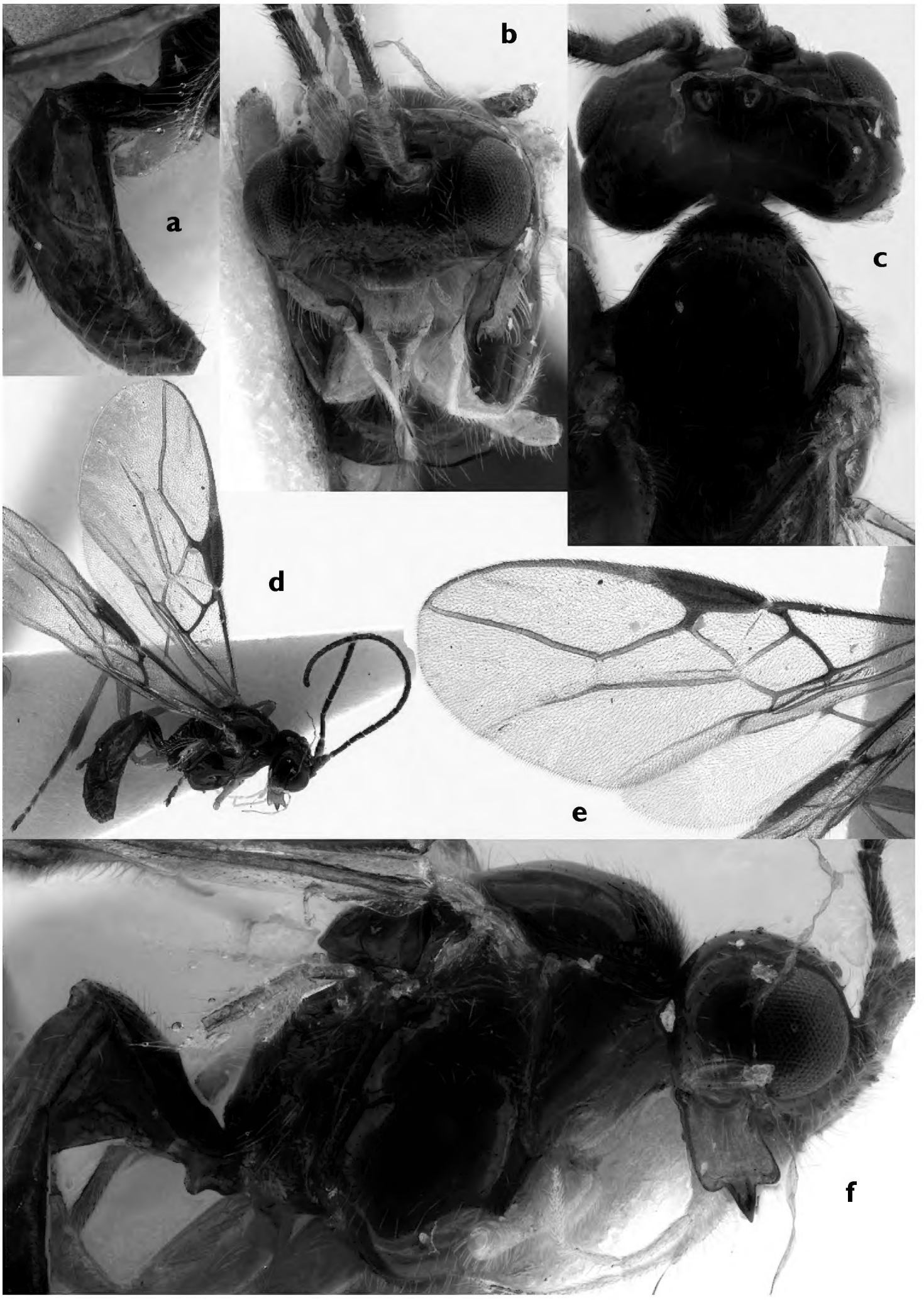

Figure 2. Montage of photographs of the male paratype (Sample ID MZH_GQ.22) of *M. chandleri* **a** lateral metasoma **b** face **c** dorsal head and mesosoma **d** whole insect **e** wing **f** lateral head and mesosoma. The length of the body (excluding antennae) is 3.3 mm.

1.6 times longer than maximum width which is 1.3 times basal width, finely rugulose and setose; three teeth with the central pointed and 0.3 times mandible length, the others obtuse and slightly reflexed relative to the axis of the mandible, no sharp incisions between teeth; head 1.3 times as wide as mesoscutum.

Mesosoma. Length of mesosoma 1.25 times its height; pronope absent; side of pronotum glabrous and largely smooth with some crenulation antero-medially and ventrally; mesopleuron smooth with scattered setae, mesopleural sulcus finely crenulate, precoxal sulcus completely absent; mesosternum with moderately dense posteriorly directed setae and a narrow punctate sulcus; metapleuron shallowly rugulose with sparse setae; mesoscutum with a triangular area of dense setae and punctation on its anterior surface extending somewhat dorso-medially, but dorsal surface largely shiny with sparse setae, notauli punctate anteriorly but absent from dorsal surface, a medio-posterior groove runs from 2/3 to posterior edge, margin adjoining pronotum with longitudinal striae; scutellar sulcus 3.0 times as wide as long, with a strong medial carinae and two pairs of weaker lateral carinae; scutellum smooth with a few setae; axillar depression well developed and weakly crenulate; metanotum rugose with an indistinct antero-medial carina that bifurcates posteriorly, not protruding in lateral view; propodeum rugulose anteriorly, medially and laterally, with a relatively smooth area latero-medially, posterior region adjacent to insertion of first metasomal tergite incised and raised with horizontal striae, lateral posterior margin with small protuberance, surface with scattered sparse setae.

Wings. Fore wing: closed marginal, three submarginal, discal and subdiscal cells; pterostigma sub-elliptical, about 4.5 times as long as maximally wide, *r* inserted at about 0.4 times the length of the pterostigma, anterior ventral margin of pterostigma before insertion convex, beyond insertion it narrows and merges gradually with *1-R1*; length of *r* 0.6 times the width of pterostigma, approximately orthogonal to anterior wing margin; ratio of *r: 3-SR: SR1* = 1: 5.2: 9.3, *SR1* slightly sinuate ending near wing apex; second submarginal cell narrows distally, 5-sided (i.e. *m-cu* postfurcal), ratio *2-SR: 3-SR: r-m: 2-M* = 1: 1.45: 0.46: 2.16, angle subtended by *2-SR* and *3-SR* 125°, *2-SR* slightly sinuate; *1-CU1* very short; *3-CU1a* 1.3 times longer than *CU1b*; *CU1a* concave down and extends nearly to wing margin. Hind wing: closed basal cell; *cu-a* and *2-M* present.

Legs. Hind coxa smooth; hind femur ~ 5 times longer than maximally wide, densely clothed with short setae dorsally projecting at an angle of 30°, ventrally approximately half the width of the femur and projecting at 60°; hind tibia slender, densely clothed with setae (projecting at 30°), 1.15 times longer than tarsi; apical tibial spur inconspicuous, less than 0.2 times length of basitarsus; tarsi with similar setae to tibia, tarsal segment length ratios 1 (basitarsus): 0.53: 0.42: 0.31: 0.38; tarsal claws and arolium well developed and 0.75 times length of fifth tarsal segment; structure of fore and mid legs similar though femur more slender and legs shorter, ratio of hind: mid: fore femur 1: 0.90: 0.81.

Metasoma. Length of first tergite 1.7 times its apical width, the latter 1.7 times its narrowest width near its base, a pair of dorsal carinae arise basally from the lat-

eral carinae and reach the dorsum at about ¼ and run close together in parallel to about ½ where they lose their distinctiveness, posterior dorsal surface with longitudinal sculpturing and sparsely scattered setae, a distinct dorsope present; metasoma beyond first tergite strongly lateral compressed with a strong dorsal medial carina extending from the third tergite to the end; second tergite smooth; scattered setae on second and posterior tergites; ovipositor straight and projecting, its exposed setose part 0.7 times the length of the hind tibia; ovipositor sheath with posterior directed setae projecting at an angle of 60–80°, their length up to twice the width of sheath; hypopygium slightly postero-ventrally produced, terminating at level of the cerci.

Colour. Head, mesosoma and metasoma dark brown except for yellow brown parts: scape, pedicel, base of the third antennal segment, mandibles (apart from tooth tips) and ventral part of gena, latero-ventral prothorax, tegulum, medio-ventral region of the laterally-compressed metasoma; precoxal area of mesopleuron slightly lighter than the remainder of the surface; palps and legs yellow, the mid and hind tarsi slightly darker, areola contrastingly dark brown; wing venation and pterostigma dark brown, wing membrane hyaline.

Variation amongst females. The French and Netherland female specimens generally match the holotype. The number of antennal segments were 34 and 37 (two specimens without complete antenna); extent of setation on dorsal surface of mesoscutum varies from comparatively well developed as shown in holotype (Fig. 1) to largely restricted to a few remote setae as figured in the male paratype (Fig. 2). In addition, the medio-longitudinal carina of propodeum is weakly developed in some specimens.

Description of male. ***Paratype***, ♂, length of body 3.3 mm, of fore wing 4.1 mm (Fig. 2).

This specimen is somewhat damaged with both antennae truncated and some legs missing. Similar to the female but differing in the following features.

Head. Posterior ocelli slightly closer together (OOL 3.4 times POL); face somewhat less setose.

Wings. Veins thicker than in female; second submarginal cell slightly shorter – ratio of *r: 3-SR: SR1* = 1: 4.3: 8.3, ratio *2-SR: 3-SR: r-m: 2-M* = 1: 1.37: 0.38: 2.06.

Legs. Hind leg first tarsal segment slightly longer – tarsal segment length ratios = 1 (basitarsus): 0.50: 0.36: 0.26: 0.34.

Mesosoma. Anterior surface of mesonotum setose but setae extending less onto the dorsal surface than in the female holotype; propodeum smoother.

Metasoma. The metasoma is not laterally compressed and does not have longitudinal carinae on the posterior tergites; thus, having a "normal" Alysiini appearance.

Colour. Ventral margin of clypeus yellow; metasoma more uniformly brown.

Molecular analysis. Sequence data from the mitochondrial CO1 gene (the standard barcode locus) were obtained from the *M. chandleri* holotype (607 base pairs) and a British specimen of *M. indagatrix* (550 b.p.). A male Finnish specimen with identical gene sequence to the holotype was found in the BOLD database. No further Old World sequences were present in BOLD, but it did contain seven closely-related

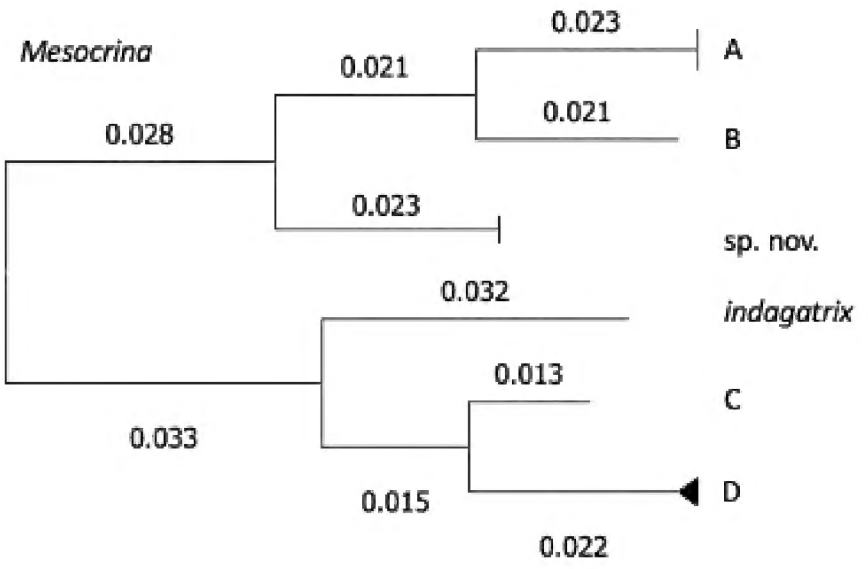

Figure 3. Maximum-likelihood tree (CO1 gene, Tamura-Nei model) with branch lengths of the 10 *Mesocrina* sequences in the BOLD database. The height of the terminal triangular wedges represents sample number and their horizontal width the genetic variation within the species (where no variation the wedge is a vertical line). Letters represent putative and undetermined Canadian (**A, B, D**) or Californian (**C**) species of *Mesocrina*.

North American sequences, some identified as *Mesocrina* and others that appeared from images in BOLD to belong to the genus. A maximum likelihood phylogenetic tree (CO1 gene, Tamura-Nei model; default MEGA settings) of the 10 sequences was created (Fig. 3), and they segregated into six putative species or BINs (Barcode Index Numbers; BIN codes as of February 2024).

Mesocrina chandleri (BIN: BOLD:ADX0117) shows a 6.5% divergence from its nearest relative, a Californian BIN (BOLD: AFO2946) represented by a single specimen. The two together with a Canadian BIN (3 specimens, BOLD:ACD3275) form a clade separated by 6.1% from a clade containing *M. indagatrix* (BOLD:AED2809) and two Canadian BINs (BOLD:AAU8494 & ACL6319). *M. indagatrix* shows a 11.6% separation from *M. chandleri* and 6.0% from the nearest Canadian BIN. The genetic data thus strongly supports the distinctiveness of the new species.

Discussion

The Palaearctic species of *Mesocrina* Foerster can be distinguished by the following key which is based on Belokobylskij's (1998) key (in Russian).

1 Precoxal sulcus distinctly crenulate; posterior surface of propodeum sloping vertically; first metasomal tergite about as long as its apical width; mesoscutum, pronotum and mesosternum brownish yellow; propleuron brownish; [vein r of fore wing much longer than wide; vein 1-SR short]; India, N. China (Jilin, Fujian, Hainan, Yunnan)..... ***M. dalhousiensis*** **Sharma, 1978**

– Precoxal sulcus smooth or absent; propodeum gradually sloping posteriorly; first metasomal tergite 1.2–2.0 times as long as its apical width; at most the pronotum ventrally, and the propleuron, brownish yellow **2**

2 Setose part of ovipositor sheath about as long as first tergite, 0.3–0.5 times as long as hind tibia (and shorter than apical height of metasoma and 0.13–0.14 times as long as fore wing); anterior half of middle lobe of mesoscutum largely glabrous and without distinct punctures; Palaearctic & NE Oriental; Fig. 4 ..... ***M. indagatrix* Foerster, 1863**

– Setose part of ovipositor sheath 1.5–2.0 times as long as first tergite, 0.7–0.9 times as long as hind tibia (and about equal to apical height of metasoma and about 0.2 times as long as fore wing); anterior half of middle lobe of mesoscutum more or less setose and with some punctures..... **3**

3 Third antennal segment about 1.2 times longer than fourth segment; third tooth of mandible much smaller than first tooth; pterostigma robust and strongly sclerotised, about 5.0 times wider than length of vein r; [clypeus blackish]; East Palaearctic..... ***M. lesovik* Belokobylskij, 1998**

– Third antennal segment 1.5–1.7 times longer than fourth segment; third tooth of mandible similar to first tooth or larger; pterostigma more slender and less sclerotised, about twice times wider than length of vein r..... **4**

4 Mandible less robust, with first tooth of mandible not protruding and similar to third tooth; vein 2-SR of fore wing distinctly sinuate; antenna with 31–32 segments; propodeum without sculpture medially; East Palaearctic..... ..... ***M. licho* Belokobylskij, 1998**

– Mandible more robust, with first tooth of mandible rather protruding and sometimes larger than third tooth; vein 2-SR of fore wing straight or slightly sinuate; antenna with 34–40 segments; propodeum more rugulose or with carina medially..... **5**

5 Vein r of fore wing 0.8 times maximum width of pterostigma and narrow; first metasomal tergite 1.1 times as long as apically wide, twice as wide posteriorly as minimum width; propodeum with distinctly developed medio-longitudinal carina; clypeus largely yellow; second submarginal cell of fore wing robust and vein SR1 about 2.2 times as long as vein 3-SR; [middle lobe of mesoscutum only anteriorly setose (confined to anterior edge)]; East Palaearctic..... ***M. leshii* Belokobylskij, 1998**

– Vein r of fore wing thickened and 0.3–0.6 times maximum width of pterostigma; first metasomal tergite 1.7 times as long as apically wide, 1.7 times as wide posteriorly as minimum width; propodeum at most with weakly developed medio-longitudinal carina; clypeus dark brown or yellowish near ventral rim; second submarginal cell of fore wing less robust and vein SR1 1.7–2.0 times as long as vein 3-SR; [linear medio-posterior depression deep and comparatively long; females with 34–37 antennal segments; setose area of middle lobe of mesoscutum variable]; West Palaearctic; Figs 1, 2..... ***M. chandleri* sp. nov.**

In Europe only *M. indagatrix* (Fig. 4) and the new species are currently known. Females of *M. chandleri* are easily distinguished by their longer ovipositor. Males are harder to tell apart, but *M. indagatrix* is somewhat smaller and the anterior of the mesoscutum middle-lobe is smoother and bears fewer setae.

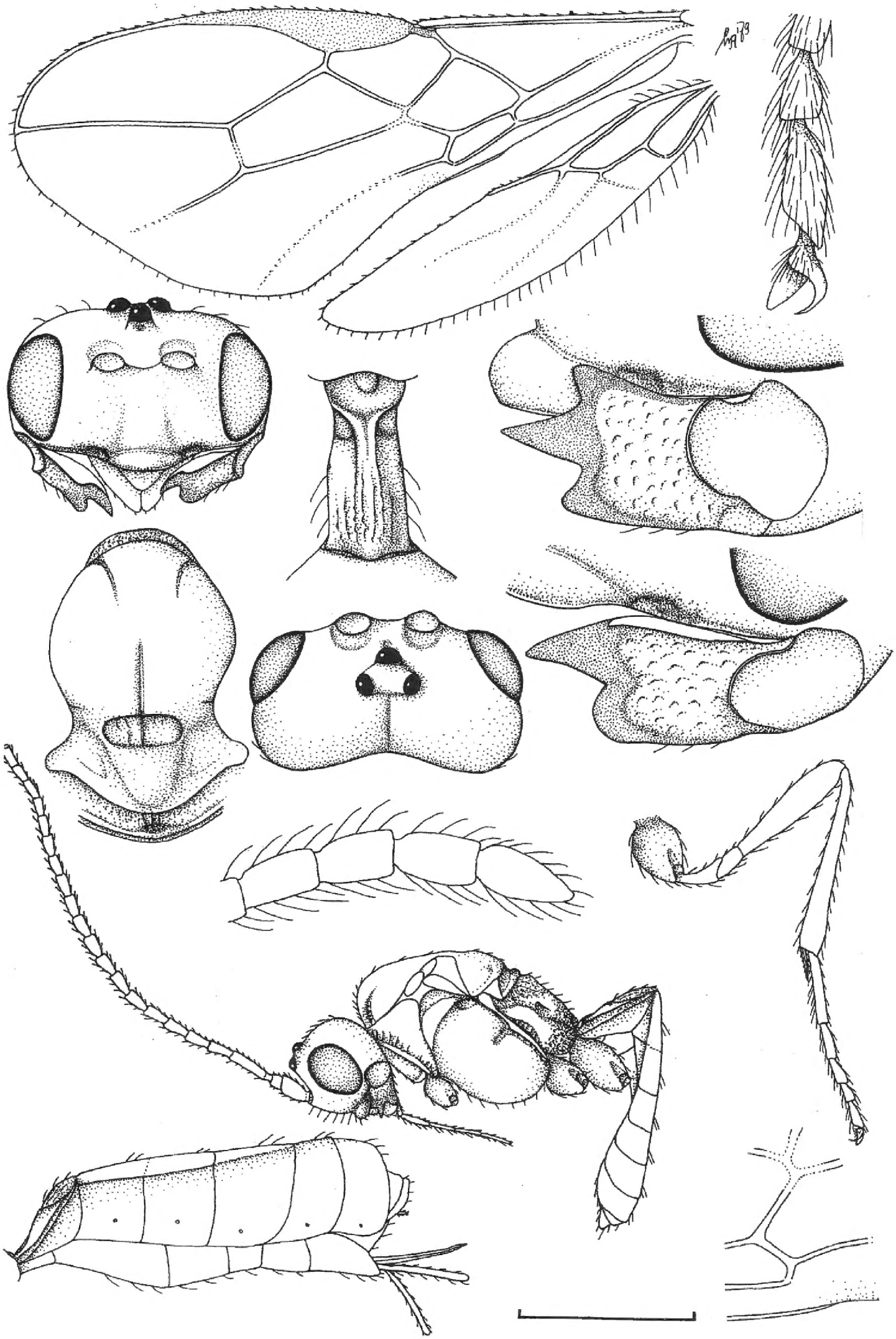

Figure 4. Montage of drawings (by C.v.A. using a camera lucida) of male and female *Mesocrina indagatrix*. Scale bar: 1.0 mm.

Females of both European species of *Mesocrina* and an American species (Wharton 1980) have been captured on gilled fungi, and it has been hypothesised that the laterally flattened female metasoma allows it to be inserted between closely packed fungal gills (Wharton 1980). We are unaware of any substantiated host rearing records but as all Alysiinae attack Diptera we presume *Mesocrina* spp. parasitise fly larvae feeding in fungal fruiting bodies.

Königsmann (1959) quotes two non-fungi-associated host records for *M. indagatrix* which he referred to as *Pseudomesocrina venatrix* Marshall, later synonymised by van Achterberg (1983). The first a male from a *Pegomya* sp. (Anthomyiidae) leaf mining *Rumex* sp. in the UK (Morley 1933). The first author and his students have reared 1880 parasitoid specimens from *Pegomya* spp. feeding on *Rumex* in the UK of which the only Alysiini were *Adelurola florimela* Haliday which made up 35% of the rearings. As males lack the distinctive compressed metasoma, and as Morley says the male only differs from the female in antennal segment number (which would be a curious observation to make about a highly sexually dimorphic *Mesocrina*), we suspect Morley's record is a misidentification, possibly of *A. florimela*. The second is *Nanna* (=*Amaurosoma*) *armillata* and/or *Nanna flavipes* (Scathophagidae) in developing flower heads of grasses, *Phleum* spp. (Poaceae), in Sweden (Borg 1959). We suspect this is a misidentification of *Synelix semirugosa* Haliday (Braconidae, Alysiinae) which attacks these hosts (King et al. 1935; Telenga 1935) and also has a laterally compressed metasoma. Our working hypothesis thus remains that *Mesocrina* spp. are parasitoids of Diptera in fungi.

The UK, Netherland and French specimens of the new species were all captured in October while the more northerly record from Finland is from September. The three specimens of *M. indagatrix* in the NMS collection were also collected in the autumn. The abundance of fungal fruiting bodies peaks at this time of year, and so the phenology and putative biology are consistent. *Mesocrina chandleri* is a relatively large and distinctive species (for an Alysiini) and given how widespread it is we are surprised it has not been noted before, especially as some of the recent records come from sites that have been regularly surveyed for Braconidae. We speculate that the species may be undergoing a current expansion of range and/or abundance.

There are currently eight described species of *Mesocrina*, six from the Palaearctic and two from the Nearctic (Wharton 1980; van Achterberg 1983; Belokobylskij 1998). However, DNA CO1 sequences of the two European species cluster closely with four North American taxa that we believe are *Mesocrina* (that may or may not include the two described by Wharton) suggesting greater diversity in the Nearctic than currently recognised.

The genus *Mesocrina* was described by Foerster (1863 [1862]) though van Achterberg (1983) treated it as a subgenus of *Dapsilarthra*. Later Papp (1991 [1990]) raised it to genus level which was followed by other authors (van Achterberg 2014). Other *Dapsilarthra* genus-group braconids attack phytophagous cyclorrhaphan Diptera and they are thought to be the sister group of the Dacnusini which have the same biology (Griffiths 1964). Van Achterberg (1983) noted that the association of *Mesocrina* spp. with fungi was atypical for the genus group, and Wharton (1980) suggested an

affinity with *Alysia* which is supported by our (relatively limited) DNA sequence data. Stronger evidence comes from a recent phylogenomic study of the Braconidae that included single species of *Alysia*, *Mesocrina* and *Dapsilarthra*: the first two genera are closely associated, while *Dapsilarthra* is distantly related and is indeed placed near the root of the Dacnusini (Jasso-Martinez et al. 2022).

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